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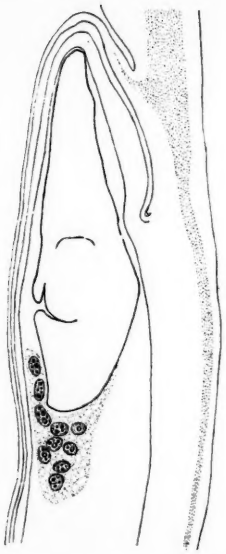

THE UNHAPPY UPSIDE DOWN HYBRID EMBRYO
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Cytology in 1944

"Twinning" in Cotton

Selection for Qualitative Characters

Population Arithmetic and Geometry

The All-Different Schense Quadruplets

VOLUME 35 MARCH, 1944 NUMBER 3

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The
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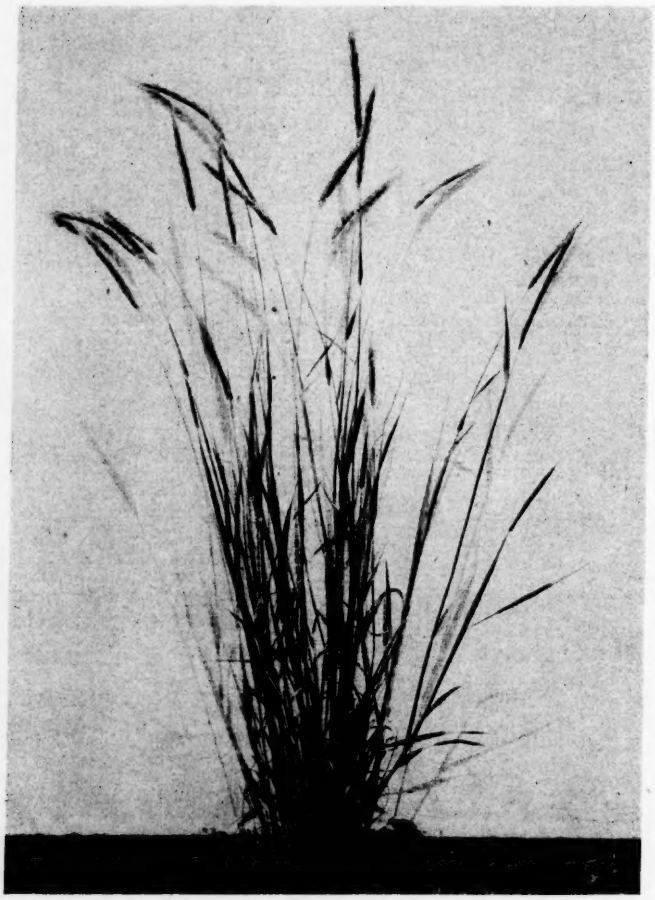


FROM 81 HYBRID SEED, ONE SURVIVOR

Figure 1

This plant is the only surviving hybrid of squirrel-tail grass and rye (*Hordeum jubatum* × *Secale cereale*). It was produced by removing the embryo while still very small from the seed, and raising it artificially in a botanical "incubator." Removed from the fatally incompatible tissue of the hybrid endosperm, this one seed out of 81 thus treated came through to adult development.

A HYBRID BETWEEN *HORDEUM JUBATUM* AND *SECALE CEREALE*

Reared from an Artificially Cultivated Embryo*

R. A. BRINK, D. C. COOPER AND L. E. AUSHERMAN
University of Wisconsin

THERE is now substantial evidence that the dominant tissue in the juvenile seed is the endosperm, a tissue that arises from the unique secondary fertilization occurring in the flowering plants. Furthermore, it is becoming increasingly apparent that when the crossing of distantly related species gives rise to a seed which collapses, the breakdown is an expression of hybridity in the endosperm rather than in the zygote. The facts suggest an important generalization relating to reproduction in this group of organisms: namely, that the capacity for development of the seed to a germinable condition and the inherent viability of the contained embryo vary independently of each other to a significant degree. A logical deduction from the above hypothesis is that, if suitable means of cultivating artificially the excised immature embryos are available, various hybrids whose development is terminated naturally in the seed may be grown to maturity. That Laibach[10] and Skirm[14] have succeeded in particular instances in rearing interspecific hybrid embryos on nutrient media points to the correctness of this inference. Additional tests are desirable, especially in those cases wherein the course of development leading to failure of the seed has been studied. There are probably fairly restricted limits to the inherent viability of interspecific hybrid embryos themselves. How wide are these limits relative to those set by the endosperm? An answer to this question calls for a knowledge of the developmental behavior of interspecific hybrid seeds as well as of the extent to which the embryos excised from them are cultivable. The present investigation, which was planned with this dual objective in mind, deals with the rearing by artificial means of a hybrid between *Hordeum jubatum,* the squirrel-tail grass of the roadside, and *Secale cereale,* common rye. Observations on the cytological behavior of the hybrid plant are also reported.

Development of the Hybrid Seeds

Hybridization between *H. jubatum* and *S. cereale* is rather easily effected. Quincke[13] found that about 95 per cent of the florets set seed when *H. jubatum* is used as the pistillate parent in the mating. We, likewise, have obtained a high percentage of fertile ovules on crossing local squirrel-tail grass plants with the Imperial variety of rye. Gametic union occurs within four hours after pollination, as in *H. jubatum* selfed. The reciprocal cross, *S. cereale* ♀ × *H. jubatum* ♂, was not attempted.

The hybrid seeds begin growth promptly, and continue development for varying periods of time. Many collapse within six days. Others may persist for as long as 13 days. Histological observations indicate, however, that probably no embryos remain alive much beyond this period. At maturity even the largest seeds are much shrivelled and all attempts to germinate them have failed.

Microscopic examination shows that many hybrid embryos make considerable growth before death occurs. Such an embryo in a six-day old seed is illustrated in Figure 2. In general, the rate of development of the hybrid embryo is lower than that of *H. jubatum.* After a given period of time following fertiliza-

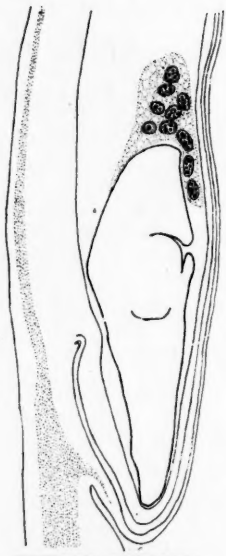
*Papers from the Department of Genetics, No. 325, Agricultural Experiment Station, University of Wisconsin. The writers desire to acknowledge the support provided by a grant-in-aid from the Rockefeller Foundation.

tion the hybrids tend not only to be smaller but also less differentiated than selfs. This does not necessarily mean, however, that the hybrid embryos are intrinsically weak. Perhaps they are retarded mainly as a result of circumstances in their local environment. A study of the cause of failure in the *H. jubatum* × *S. cereale* seeds, being published elsewhere, indicates that the lag in embryo development is a consequence of the abnormal behavior of other tissues of the seed, particularly the endosperm. In this respect the case offers a parallel to the examples of seed failure following interspecific hybridization in *Nicotiana* described earlier by Cooper and Brink[3] and Brink and Cooper.[4] The histological evidence suggests that the young hybrid embryo, if freed of its unfavorable environment in the seed, is capable of further development. A direct verification of this conception was sought in attempts to cultivate the incompletely developed *H. jubatum* × *S. cereale* embryo on an artificial medium.

The embryos were grown on a medium whose inorganic constituents conformed to those of White's[20] formula. Three solutions, *A*, *B* and *C*, containing the major mineral elements required for plant growth were made up as follows:

A.	$Ca(NO_3)_2 \cdot 4H_2O$	.142 g.
	$MgSO_4 \cdot 7H_2O$	.074 g.
	KNO_3	.081 g.
	KCl	.065 g.
	Distilled water	250 cc.
B.	KH_2PO_4	.122 g.
	Distilled water	100 cc.
C.	$Fe_2(SO_4)_3$	.240 g.
	Distilled water	100 cc.

Ten cc. of solution *B* and one cc. of solution *C* were combined with 250 cc. of solution *A*. Twenty grams of cane sugar and 250 cc. of a two per cent agar solution were then added. A yeast extract was used as a source of the minor growth elements. A half-cake of yeast was macerated in 500 cc. of water and boiled for 30 minutes. The starchy material present was removed by centrifugation and 10 cc. of the extract was added to the above mixture. The total volume was then brought up to one liter with water. The pH was adjusted to 5.7-6.3 by the addition of KOH. The nutrient medium was placed in 10 cc. vials, about two cc. per vial. The vials were then stoppered with cotton and sterilized at 15 lbs. pressure for 20 minutes in an autoclave.



HYBRID EMBRYO

Figure 2

Section through the apical portion of a six-day-old seed with an embryo in an early stage of development. Above it is the shrinking multinucleate endosperm closely associated with the scutellum. In the normal embryo the endosperm would fill all the space above the embryo. × 150.

Growth of the Excised Embryos

Hybrid embryos were dissected from 9-, 10-, 11- and 12-day old seeds which had been immersed in 1-1000 mercuric chloride solution for 2-3 minutes. They were then placed on the surface of the medium and incubated at room temperature in weak daylight. Of the 81 embryos thus treated, 34 proved to be free from contamination with fungi and bacteria. The embryos when first removed from the seeds were just visible to the naked eye. All that were free from contamination made considerable growth on the nutrient medium. The growth was of an undifferentiated character in most cases. One embryo, however, differentiated in the normal way and eventually put forth roots and a shoot. This seedling was potted off at the three-leaf stage and placed in a relatively cool greenhouse in late October.

A Hybrid Plant

Growth of the hybrid seedling was limited during the short days of autumn and winter, and the plant became rather chlorotic. In fact many leaves turned yellow and died. With the advent of the longer days of spring, however, the vigor of the plant distinctly improved and new shoots at the crown were freely produced. Fairly rapid growth occurred following transplanting out-of-doors in April, and flowering stems appeared in mid-July. The photograph shown in Figure 1 was taken on July 28 at the full-bloom stage. The plant was about two feet high at this time, of a normal green color, and in a thrifty condition.

Although the plant flowered freely, no seeds were formed. A typical barren head from the hybrid is represented in Figure 4 in comparison with normal mature heads from the respective parental species.

Since plants of the parental species, *H. jubatum* and rye, were not carried forward under conditions comparable to those under which the hybrid developed, a fair comparison of size and rate of growth cannot be made. The relatively weak condition during the seedling stage indicates, however, that the hybrid was probably somewhat inferior in capacity for growth to the pure species concerned. Nevertheless the fact that a hybrid was grown out to the flowering stage makes it clear that the intergeneric combination is not lethal for the zygote in a direct sense. Death of the embryo in the seed must arise from some other cause.

Cytological Behavior of the Hybrid

The somatic chromosome number in *Hordeum jubatum* is 28 and that in *Secale cereale* is 14. The hybrid plant proved to have 21 chromosomes (Figure 3*A*), as expected. The behavior of the chromosomes in the hybrid at microsporogenesis is of interest for the light it throws on the apparent lack of homology between the two complements which have been brought together in this plant, presumably for the first time. The mode of association between the two groups of chromosomes, however, is not directly discernible because the rye and *H. jubatum* chromosomes are so nearly alike in size and form. One might expect on the simplest assumptions either that: (1) the seven rye chromosomes would pair with a like number of *H. jubatum* chromosomes (allosynapsis); or (2) that autosynapsis would occur among the *H. jubatum* chromosomes. In either of these events seven univalent chromosomes would be found. The actual relationship, however, is found to be more complex.

Diakinesis stages usually exhibit five bivalents and 11 univalents (Figure 3*B* and *C*). The pairing chromosomes are very loosely associated at this stage. The five bivalents become oriented on the heterotypic equatorial plate well in advance of the univalents (Figure 3*D*). They disjoin and are at a mid-anaphase stage by the time the univalents become oriented on the plate (Figure 3*E*). In many cases one or more of these bivalents fails to disjoin completely (Figure 3*F*) and, as a result, bridges are formed between the interphase nuclei (Figure 3*G*). This is an indication of partial homology between the bivalent chromosomes involved. Following crossing over, the chiasmata fail to terminalize beyond certain points leaving the members of the pair attached which accounts for the failure of disjunction and the occurrence of bridges.

The univalent chromosomes behave irregularly at metaphase I. They are loosely associated with the bivalents and some of them come to occupy the equatorial region as the members of the bivalents are approaching the poles. These chromosomes split longitudinally and the daughter chromosomes move poleward. Others move toward the poles without undergoing division. This is illustrated in Figure 3*E* where the five bivalents have disjoined and are at anaphase. Ten longitudinally split univalents occupy the equatorial plate and one univalent (*a*) is near the pole. One or more nuclei are formed in each daughter cell during interphase (Figure 3*F* and *G*), two of the nuclei usually being

CHROMOSOMES OF THE BARLEY-RYE HYBRID

Figure 3

A shows a somatic equatorial plate with 21 chromosomes. Fourteen of these are contributed by the *Hordeum* parent and seven by the *Secale* parent. × 1450. The remaining figures show microsporogenesis in the hybrid. *B* and *C* show diakinesis, five loosely associated bivalents and 11 univalents are present. *B-J* all × 775. *D* shows a heterotypic equatorial plate with bivalents on the plate and irregularly arranged univalents. *E* represents a somewhat later stage of the heterotypic anaphase. The five bivalents have disjoined and are approaching the poles, but the longitudinally split univalents have only just become oriented on the equatorial plate. One bivalent pair has failed to disjoin completely, so that the two anaphase groups are united by a bridge. One univalent (*a*) has passed to one pole without splitting. *F* shows a heterotypic telophase. A cell plate is forming across the equatorial region. The two daughter nuclei are connected by a chromosome bridge. *G* shows the same at a somewhat later stage. One cell is equipped with one nucleus while the other has two. There is a bridge of chromatin material between the single nucleus in one cell and the smaller nucleus in the sister cell.

H—Homoeotypic anaphase. The chromosomes which disjoined as bivalents and the univalents which passed to one or the other pole without splitting at heterotypic anaphase have split and moved poleward. The univalents which split in the preceding division are irregularly

connected by a nuclear bridge formed as a result of the failure of complete disjunction of certain of the bivalents.

The chromosomes which disjoin as bivalents split and separate on the homoeotypic equatorial plates as do the univalents which pass to one or the other pole of the heterotypic spindle without splitting (Figure 3*H*). The univalents which split on the heterotypic spindle become irregularly arranged on the homoeotypic spindle and lag thereon so that some of them fail to reach the pole in time to become associated with the forming daughter nuclei. They then form supernumerary nuclei of varying sizes depending on the number of chromosomes which become associated at that time (Figure 3*I*). These supernumerary nuclei are easily distinguished from those which are formed from the products of the meiotic divisions since the chromatin remains densely compact and takes a very deep stain. In a few instances most if not all of the chromosomes passed to one pole of the heterotypic spindle and, as a result, one spindle of the homoeotypic division had few or no chromosomes and the greater number of chromosomes were on the other spindle (Figure 3*J* and 3*N*). Twenty chromosomes were on the one spindle (Figure 3*K*) in the first case and a single chromosome on the sister spindle whereas in the second case all 21 chromosomes were on the one spindle (Figure 3*O*) and there were no chromosomes in the sister cell.

A varying number of nuclei are present in the spores at the tetrad stage (Figure 3*P*). One of the 317 spores examined 13 per cent had a single nucleus (Figure 3*L*), 39 per cent had two nuclei (Figure 3*M*), 31 per cent had three nuclei (Figure 3*Q*) and 13 per cent had four nuclei (Figure 3*R*). The number of nuclei in the remaining spores ranged from five to seven. Even at this late stage of development the micronuclei remain in a more or less condensed condition. The spores disintegrate shortly after their formation and no well developed pollen grains can be found.

These observations indicate that at most the homology between the *S. cereale* and *H. jubatum* chromosomes is not close. If the five bivalents formed arise as a result of autosyndesis of *H. jubatum* chromosomes, leaving the rye chromosomes unpaired, it could be concluded that the latter bear little correspondence to the former. On the other hand, if the bivalents result from synapsis between members of the two species complements, two rye chromosomes do not find mates and those which pair do not always establish a normal association as shown by the frequent occurrence of chromatin bridges. The highly abnormal nuclear condition of the microspores and the sterility of the plant are additional indications of non-homology between the *S. cereale* and *H. jubatum* chromosome complements.

This behavior of the chromosomes at meiosis closely parallels that described by Myers[12] for the hybrids which he obtained following the cross *Phleum pratense* ($n = 21$) $\times$ *P. subulatum* ($n = 7$). He likewise found that both bivalents and univalents at metaphase I. The bivalents separated at anaphase I,

arranged in the mid-regions of the spindles. *I*—Homoeotypic telophase. Each spore has one central nucleus and one or more nuclei of varying sizes formed from the chromosomes which lagged on the spindle. *J*—Homoeotypic metaphase. Twenty of the chromosomes passed to one pole at heterotypic anaphase and one chromosome passed to the opposite pole so that interphase nuclei, one containnig 20 chromosomes and the other a single chromosome were formed. Twenty chromosomes are present on one homoeotypic metaphase spindle and a single chromosome on the sister spindle. *K*—Detail view ($\times$ 1450) of the 20 chromosomes shown in *J*. Some chromosomes still show evidence of the paired condition. *N*—Homoeotypic anaphase. All of the chromosomes passed to one pole in the preceding division of two cells where formed, one without a nucleus. Twenty-one chromosomes are present on the spindle in the one cell. $\times$ 775. *O*—The 21 chromosomes shown on the spindle in *N*. Some chromosomes have passed poleward and others are scattered in the mid-region of the spindle. $\times$ 1450.

P—Tetrad stage. The nuclei of the individual spores vary both in size and number. $\times$775. *L-M-Q-R*—Spores with one, two, three and four nuclei, respectively. The extra nuclei vary considerably in size and in every instance are smaller than the central nucleus. $\times$775.

an occasional chromatin bridge being formed. The univalents divided equationally at anaphase I and moved poleward. A majority of the daughter univalents and the chromosomes resulting from disjunction of metaphase I bivalents became oriented on the metaphase II spindle where the latter divided equationally and moved poleward at anaphase II. The daughter univalents, on the other hand, lagged on the spindle so that quartet formation was irregular and micronuclei or chromatin clumps were present in nearly all spores.

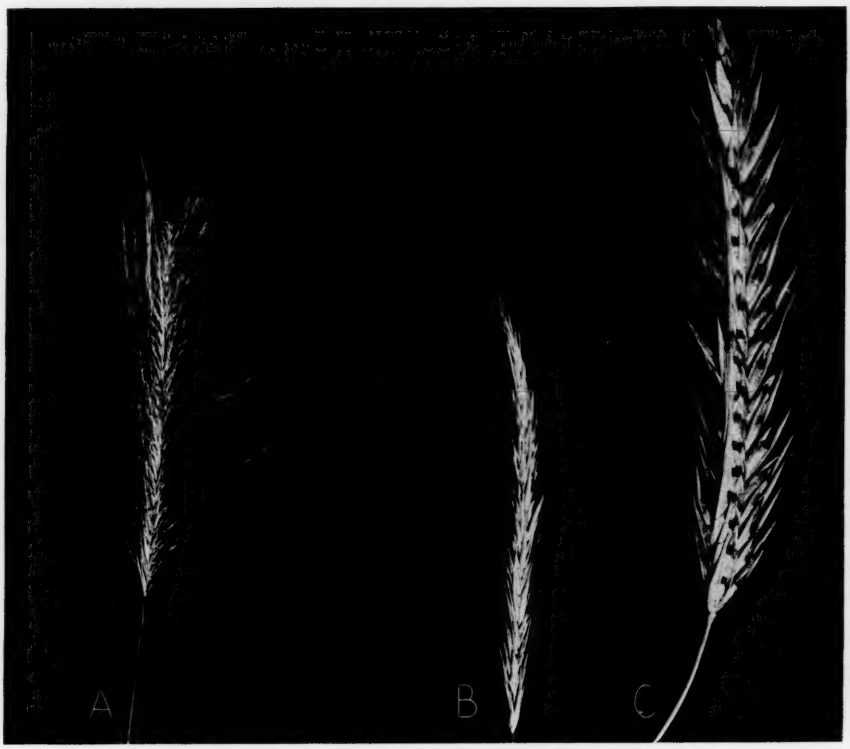
Discussion

The fact that an interspecific hybrid zygote which normally does not reach the mature embryo stage within the seed may be reared by artificial means demonstrates that viability of the young zygote is independent in some measure of the factors which govern seed development. There are two reasons why the *H. jubatum* × *S. cereale* hybrid whose propagation is discussed above, is of particular interest in this connection. In the first place, the relationship between the two parent species is rather remote as shown by the limited homology between the two chromosome complements. Secondly, as described elsewhere in detail by two of the authors,[6] the disturbance in development occurring in the seed after this mating are of an extreme character and lead to comparatively early and complete breakdown. In spite of these circumstances, however, the hybrid zygote is potentially capable of growing into a vegetatively rather vigorous, although sterile, plant. It seems clear that death of the embryo in the seed does not arise from defects inherent in the zygote but is a secondary phenomenon associated with changes in the accessory tissue of the seed.

Whether the reverse relationship in interspecific hybrids is ever true, namely, that a seed may develop which is normally constituted except that the embryo fails is not certainly known. Such seeds might be expected to occur from time to time. "Germless" kernels, with well developed endosperm, have long been familiar as recessive characters in maize,[7] although little is known of the course of development leading to the condition. According to the general hypothesis set forward by Brink and Cooper[4] regarding the significance of double fertilization and the role of the endosperm in development of the seed, embryo failure, *sui generis*, should be infrequent relative to collapse arising from hypo-function of the endosperm. The basis for this view is the primary relation of the latter tissue to morphogenesis and nurture of the seed. During its early development the embryo appears to be a highly dependent nursling of the endosperm. Later, after the endosperm disappears or—, in the few families, such as the Gramineae, in which the tissue persists—enters the storage phase, further development of the embryo may be a function principally of the genotype of the zygote itself. Embryo lethals, previously without opportunity for expression, may now manifest themselves. Seeds with abortive embryos but otherwise normal could thus arise.

The literature of plant genetics is replete with examples of seedling lethals which do not necessarily involve impairment of the seed itself. Simple recessive chlorophyll deficient types are a familiar category. Wide crosses sometimes give results of similar kind. The mating *Melilotus alba* × *M. dentatus*, for example, yields a fairly plump and readily germinable seed but the hybrid seedling is albinotic and dies early. Smith[15] has recently shown how this ordinarily lethal interspecific hybrid may be reared by grafting it upon a normal *Melilotus* plant. Genes causing defects in the photosynthetic mechanism usually express themselves only after the zygote attains an independent status. Doubtless there are many genes conditioning other vital processes which also exert their initial effects at the seedling stage.

The facts presented above show, however, that it is not justifiable to assume that collapse of the embryo within the seed is a phenomenon parallel to death of the seedling, the essential difference



MATURE HEADS OF PARENTS AND HYBRIDS

Figure 4

A—Head of *H. jubatum,* and *C*, head of *S. cereale,* with barren head of the hybrid (*H. jubatum* × *S. cereale*) in the center (*B*). The extremely abnormal chromosome distribution shown in Figure 3 resulted in a very high degree of sterility.

being merely that the genes concerned become active at an earlier stage in the ontogeny of the zygote. The analogy does not hold because the embryo is not an independent structure in the seed. It is subordinate to the endosperm. Differentiation and a large part of the total growth occur in association with the endosperm. If failure occurs within the seed, therefore, the breakdown is usually a result of endosperm disfunction.

Now the endosperm is a special tissue operating under a unique set of conditions. It is intercalated between parent sporophyte and young zygote, exerting some morphogenetic influence,[5] and obtaining from the former, and probably further elaborating, nutritive materials, which the latter requires for development. This peculiar relationship entails demands upon the tissue which the embryo does not have to meet. The double complement of inheritance of maternal origin may be an adaptation to this circumstance. Even though endosperm and embryo, aside from this difference in chromosome balance, carry the same genes in a given case, therefore, the two tissues do not necessarily stand or fall together, so to speak. The endosperm may fail in some function which the zygote is never required to perform. This appears to be the basis for the

occurrence of potentially viable embryos associated with abortive endosperms.

The endosperm-embryo relationship in the developing seed, formulated above, has significant implications which have been briefly developed in an earlier publication.[5] One of these is that the endosperm constitutes an isolating mechanism (in the sense that Dobzhansky[8] used the term) of first order importance in the flowering plants. Space does not permit an enumeration here of the many cases in the literature of hybrid incompatibility which are either known to rest upon breakdown at the seed stage or may be suspected of involving a barrier of this kind. Demonstration that failure of the seed arises from hypo-functioning of the endosperm, even in those instances in which at least some histological data are available, is by no means complete; but it seems to the writers that a mechanism that is comparable in this respect in families as widely removed from each other as are the Solanaceae[5, 4] and the Gramineae[6] is probably operative widely among the angiosperms.

A further deduction that receives direct confirmation in the present investigation is the practicability of rearing various plants not hitherto known by excising the immature embryos from the seed and cultivating them artificially. These plants fall into two general classes, (1) first generation interspecific hybrids that ordinarily die in the seed and (2) derivatives of hybrids that fail to appear in the segregating generations because the endosperms with which the embryos are associated are genetically incapable of supporting seed development to the germinable stage. Laibach[10] and Skirm[14] have described examples of the former type; and Thompson[16] shows how important elimination at the seed stage may be in narrowing the range of types emerging in the segregating generations following certain distant matings in *Triticum*. There is only a meager basis at present for estimating the extent to which the plant resources at the command of the investigator may be extended by this procedure but the possibilities appear to be much greater than could have been predicted earlier. The successful rearing of the *Hordeum jubatum* × *Secale cereale* hybrid supports this position in view of the early and complete failure of the seeds naturally and the limited homology between the two chromosome complements. There would seem to be grounds now for a fuller exploration at the hands of breeders of the possibilities for improvement inherent in interspecific hybridization than has been undertaken heretofore. Investigators should not be deterred from such a study merely because viability is only one of numerous criteria which a useful interspecific hybrid must meet. The undertaking is justifiable if viability is independent in a sufficient degree of the other important qualities. Again the available evidence is limited, but Laibach's[10] example from *Linum*, Skirm's[14] results with *Lilium*, and the present findings on a cereal cross afford some guidance. These hybrids, normally perishing in the seed, when reared artificially are found to fall within the range of known species hybrids in respect to vegetative vigor and fertility. So far as these few data go, therefore, it appears that there is no essential difference between hybrids which naturally surmount the endosperm barrier and those which may be enabled by artificial means to bypass it.

The distinction between embryos which regularly die in the seed, and those which are still alive at maturity of the fruit, even though the seed is much shrivelled, is probably one of degree. Cultivation on artificial media of the embryo from poorly developed "mature" seeds has been used by Jorgensen,[9] Tukey,[17] Blake,[2] Beasely,[1] and Lammerts[11] to rear offspring from various intra- and inter-specific matings otherwise ineffectual or yielding a very restricted sample of adult progeny. Brink and Cooper[4] have compared seed development in a *Nicotiana* interspecific mating in which only a few seeds reached a germinable

condition with another *Nicotiana* cross in which all the seeds collapsed within a few days after fertilization. Development was found to be essentially alike in the two cases except that the changes in the endosperm and associated maternal tissues which eventually restricted growth of the embryo arose sooner and became more pronounced in the mating in which the seeds all die before the capsule is ripe.

The reasons for failure of differentiation of all but one of the 34 *H. jubatum* × *S. cereale* embryos which grew on the medium we used have not been studied. It has been postulated by van Overbeek, Conklin and Blakeslee[19] and van Overbeek[18] that the very young embryo requires for continued development certain hormones which may be supplied by addition to the nutrient medium of raw coconut milk. Older embryos, on the other hand, are considered either not to require these substances or to become autotrophic with respect to them. The particular medium employed by us may have been inadequately supplied with growth substances of this kind. Obviously this is an aspect of fundamental importance for the general problem.

Summary

1. Seeds resulting from the cross *Hordeum jubatum* ($n = 14$) ♀ × *Secale cereale* ($n = 7$) ♂ do not develop to a germinable condition. Their growth ceases at from six to 13 days after fertilization.

2. Eighty-one embryos dissected from 9- to 12-day old hybrid seeds and placed upon an artificial nutrient medium behaved as follows: 47 proved to be contaminated, and were discarded; 33 made appreciable growth of an undifferentiated character; and one developed into a seedling.

3. The seedling was potted off and grown out to maturity. The hybrid had 21 chromosomes, was intermediate between the parents in habit of growth, and sterile.

4. Diakinesis stages in the hybrid usually showed five loosely associated bivalent and 11 univalent chromosomes. Chromosome bridges were common between the interphase nuclei. It is concluded that there is little homology between the parental sets of chromosomes.

5. The results are discussed in relation to the hypothesis that the capacity for development of the seed to a germinable condition and viability of the contained embryo vary independently of each other to a significant degree.

6. The findings point to the practicability of rearing various first generation interspecific hybrids and derivatives of them which ordinarily die in the seed, by excising the immature embryos and cultivating them artificially.

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"TWINNING" IN COTTON

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SEEDS containing twin embryos are of fairly common occurrence in certain of the New World (n=26) cottons. That their occurrence is constitutionally determined is clear from the strikingly different frequencies with which they appear in different lines. Thus in strains of Sea Island cotton (*Gossypium barbadense* L.) their frequency is as high as 1 in 300 to 1 in 500, whilst in strains of Egyptian cotton in the same species, and in strains of Upland cotton (*G. hirsutum* L.), they are quite uncommon. [2,3,5,6]

As Harland first pointed out, one of the twin embryos is usually considerably smaller than the other, and grows into a haploid* plant of comparatively frail habit, which flowers earlier than its normal diploid sib and is almost completely sterile. Haploids are well known in West Indian fields of Sea Island cotton under the name "man-cotton." How many of those which occur in the field originate by twinning is not known, since haploids occasionally occur in monoembryonic seeds.[3]

Nearly all of the twin pairs in Sea Island cotton are of this diploid/haploid type. Of 55 pairs which have been raised to maturity 51 were in this category, only three pairs being diploid/diploid and one haploid/haploid (combined data of Harland,[3] Beasley,[2] and Webber[6]). It is usually supposed that the diploid twin results from normal fertilization, and that the haploid arises parthenogenetically from an unfertilized embryo sac enclosed within the same integuments (polyembryonic haploidy). In this connection it is of interest that the occasional production of two embryo sacs within a single cotton ovule has been reported by Baranov.[1] Genetic evidence from one pair of diploid/haploid twins which we have recently raised supports the natural assumption that the haploid is of purely maternal origin. Their female parent was green, and was pollinated by a dominant red homozygote; the diploid twin was heterozygous red, and the haploid green.

The mode of origin of the diploid/diploid twins is not so clear, since there has been no evidence to determine whether, like the diploid/haploid pairs, they also arise from two embryo sacs, and if so whether both of them are fertilized, or only one, one member resulting from doubling of a parthenogenetic haploid. Additional possibilities are sporophytic budding, or, in the special case of identical twins, cleavage of a single zygote. Recently we have observed a case of diploid/diploid twinning in *G. hirsutum* which is of significance in this connection. An American Upland variety, Acala Okra, having white pollen and a laciniated leaf, was emasculated and crossed with a strain of U4 (African Upland) having yellow pollen and a broad leaf. Pollen color and leaf shape are independent characters known to be inherited monogenically. Among the hybrid seeds obtained, one gave rise to twin seedlings. Both proved to be diploids, but they were not identical as would be expected from normal fertilization. One of the twins had the expected hybrid constitution since it had yellow pollen and an intermediate leaf shape. The other had the pollen color and leaf shape of the maternal parent and must therefore have arisen either sporophytically or by doubling of the chromosome complement of an unfertilized egg. In view of the predominance of diploid/haploid twinning in the New World cottons, the latter is by far the more plausible interpretation.

*In this note the terms haploid and diploid in relation to twinning refer to the chromosome number of the species concerned, and not to the basic number in the genus as a whole.

Twins in Asiatic Cottons

Twins are much less common in the cultivated Asiatic (n=13) cottons, *G. arboreum* L. and *G. herbaceum* L. In one year's sowing at this Station, only one pair of twins was observed in 40,000 seeds, and throughout the last ten years only nine pairs of Asiatic twins have been found. All occurred in pure *arboreum* material, or in material predominantly *arboreum* with traces of *herbaceum* or *anomalum* (Wawra and Peyr.) in its ancestry. The twins have occurred sporadically in different lines, giving no indication of the existence of particular high-twinning strains, like the Sea Islands amongst the New World cottons, so that their occurrence may be regarded as a haphazard phenomenon in these species.

In six of the nine pairs of Asiatic twins the two embryos were approximately equal in size, and in four of them both members were raised to maturity and were both diploid. In each of the other three pairs one member was considerably smaller than its partner; both members were raised to maturity in two of these cases. In one pair both members were diploid, and the other pair affords the only possibility of a case of diploid/haploid twinning in the Asiatics. The smaller member of the pair made poor growth, and on flowering had contabescent anthers (as in the case of haploids in Sea Island), but died before a cytological examination was made (cited by Skovsted[5]). Evidently in the Asiatic cottons diploid/diploid twinning is the general rule.

Three of the five diploid/diploid pairs which were raised to maturity afforded some genetic evidence as to their mode of origin. In two cases the twins were the result of cross-pollination after emasculation, and each member of both pairs carried alleles (leaf shape in one case, anthocyanin in the other) derived from both parents. In neither case, therefore, could one member of the pair have arisen by doubling of a haploid, as was the case in the New World pair, nor could sporophytic budding have been concerned. The twins could only have arisen either as a result of normal fertilization of two embryo-sacs, or, since in each case they were identical, by cleavage of a single zygote. The third pair of twins under discussion was derived by selfing a multiple heterozygote. The members were dissimilar in three independent main genes, and could not therefore have been monozygotic in origin. The fact that neither was identical with the parent rules out the possibility of sporophytic budding. Unfortunately in this case both twins were not tested for heterozygosity, and the possibility that one of them might have resulted by doubling of a haploid cannot be eliminated. If, however, both resulted from fertilization, their phenotype was consistent with the possibility that the two male nuclei concerned were of the same genotype, as would be likely. Of the possible mechanisms only one is common to all three cases of twinning, and that is dual fertilization.

Summarizing, twinning in the Sea Island cottons is considerably more frequent than in other types of cultivated cottons for which data are available. In the Sea Islands, most twin pairs are diploid/haploid, and the few cases of diploid/diploid twins which occur probably start off as diploid/haploid. In the Asiatic cottons twins are predominantly of the diploid/diploid type, and both members are most probably the result of fertilization. The New World and Asiatic cultivated cottons are respectively tetraploid and diploid, but it would be unwise to assume at this stage that the difference in type of twinning which they exhibit is a function of degree of ploidy, especially in view of the fact that the only case of twinning which has been reported amongst the wild diploid species (*G. sturtii* F.v.M.; Webber[6]) was of diploid/haploid nature. The balance of evidence at present suggests that the difference is genotypically controlled.

Value of Haploids

Harland[3] suggested that induced chromosome doubling in a haploid with the immediate production of a pure line as a result would be of practical importance to the plant breeder. Beasley[2] has suc-

cessfully produced pure lines of Upland and Sea Island strains by colchicine treatment of haploids, and a pure line of St. Vincent Sea Island (V135) has also been produced at this Station by the same method. It is doubtful, however, whether a pure line has any great practical advantage over moderately heterozygous material. Hutchinson[4] has stressed the point that average performance of the population is the important factor, and that residual variability may be advantageous in "buffering" environmental fluctuations. Nevertheless, artificial doubling of haploids might on occasion provide a short cut in isolating strains from highly heterozygous material. Another possible use for a doubled haploid is as an indicator of the magnitude of environmental heterogeneity. As such it could serve as a control in progeny row breeding.

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LIFE-FACTS AND THE NEW HORIZONS

Writing in the Scientific Monthly *for January, 1944, Dr. Karl Sax reviews some of the biological and geographical realities which must form the basis for a peaceful and prosperous world order. Without attempting to give a complete synopsis of his presentation, the following paragraphs (mostly direct quotation, rearranged and much condensed) give the gist and the flavor of this challenging statement.*—Ed.

Rate of Population Growth

Man lived and multiplied on this earth for five hundred centuries before the population reached 850 million people. But at the end of one additional century the population had doubled. During the recent past the world population has been increasing at the rate of one per cent a year, a rate which would nearly double the present population before the end of this century. There are now 40 persons per square mile of land area in the world. The population density of the United States is almost exactly that of the world as a whole. * * * Many misguided optimists believe that there will always be enough for all regardless of the number of people who occupy the earth. Such optimism is not limited to newspaper columnists such as Dorothy Thompson who assure us that there is "enough for all" in this world of modern science. J. B. Bernal, a reputable English scientist, suggests that if we could convert coal and limestone into food materials "we should have enough food for a population thousands or millions of times that which exists at present." An increase of one thousand times would establish a population density of forty thousand persons per square mile of land surface of the world, while an increase of a million times would mean that there would be less than one square foot of land area available for each person!

The Agricultural Outlook

The total area of all crop land in the world is about four billion acres, according to Dr. H. H. Bennett, Head of the United States Soil Conservation Service. The world's population is now over two billion, so that the cultivated land per capita is only two acres. There is more land that can be cultivated in many parts of the world, but most of it can be farmed only with diminishing returns or a much greater cost of production. Many regions of the world are already over-populated on the basis of domestic agricultural production. With the exception of Russia, practically all the nations of Europe and Asia are no longer able to produce enough food to maintain adequate nutritional standards.

Food production in Asia cannot be increased appreciably. The United States can produce more food but not enough to feed many more people here or abroad. Half the land now in use is subject to erosion or too poor to farm properly and should be retired from cultivation. Of the land not now cultivated, less than 50 million acres could be used. At present, we use over three acres of arable land per person and still we do not provide adequate food for a large part of our population. The reduction of animal product in our diet would relieve more of the basic food crops for human consumption. Such a diet would be as satisfactory as that enjoyed by the European peasant or the Asiatic coolie, although it might be more monotonous.

Meeting Population Pressures

The over-crowded nations of Europe have followed three methods to escape over-population. Industrialization and modern methods of transportation have enabled these nations to maintain populations even though food requirements exceed their own agricultural production by importing food in exchange for manufactured products. Emigration has been the second safety valve. The third method followed by the peoples of Europe in spite of legal and religious bans and the exhortations of preachers and politicians, is the artificial reduction of the birth rate. Most of the European countries have reduced their birth rates during the past fifty years from over 30 to less than 20 per thousand.

Population pressure in Asia is even greater than it is in Europe, but nations of Asia have found no satisfactory solution. More than half of the world population lives in Asia, with little relief from population pressure by migration, industrialization or birth control. The Malthusian law operates with little restraint in continental Asia. Population has increased faster than food supply and has been held in check only by famine, pestilence, and natural catastrophy. Emigration offers little hope for Asia. And the invasion of neighboring countries already over-populated, provides no more *lebensraum* for the invader unless the peoples of the conquered nations are exterminated. Such a course, intolerable to civilized people, is not justified by any biological evidence supporting the myth of racial superiority used by the Nazis for an excuse for world dominion. Asia cannot be helped by industrialization and "increasing the standard of living." So long as birth rates of 40 to 50 per thousand persist, the population will increase just as fast as food supplies and medical science will permit.

The Birth Control Paradox

The greatest enigma of this age of science is the present status of the knowledge and practice of contraception. Public opinion surveys made by the Institute of Public Opinion and by the *Ladies Home Journal* show that more than three-fourths of the people of this country approve of the dissemination of birth control information by the medical profession and even of Government-supported birth control clinics. Dr. Pearl's data show that the majority of married women practice, or think they are practicing, some form of artificial contraception. Our archaic laws prevent the dissemination of reliable information and keep the $250,000,000 contraceptive industry on a semi-bootleg status. Nearly all the Protestant churches approve of artificially controlled birthrates, and in 1930 Pope Pius gave at least implied approval of "natural" birth control. Although the Catholic church still opposes artificial contraception it is practiced by Catholics to about the same extent as it is by Protestants of similar economic and educational status. In Boston we are nevertheless told that "birth control is against God's law."

Both families and nations are confronted by the same problems. If they have more children than they can feed and educate, living standards go down and death rates go up. But if they do control births, they may be overrun by the unrestricted breeding of their neighbors. The logical solution would seem to be the control of birthrates in accord with the national or family resources.

WHO'S GOING TO BELL THE POPULATION CAT?

To the Editor, JOURNAL OF HEREDITY:

Mr. Robert Cook's editorial, "*One* world?" not only poses very important problems, but should lead to concrete suggestions as to how those problems can be attacked. He points out that geneticists, eugenists, and social psychologists should form a team to do one part of the job. I take the liberty of doubting whether this is the team with which to start the job. It seems essential that in the beginning at any event, the conclusions from mapping of invisible worlds must be inevitable. They must not be capable of attack by any large segment of the world's population on the basis of faith as opposed to reason. Unfortunately, most views on the limitation of population are subject to exactly that sort of attack.

Suppose rather that, for the sake of argument, we assume that the world's population will increase by a net amount of 50,000 a day and suppose further that, on the average, these people require 2.3 pounds of additional food each per day. Then the 50,000 increase will require per year an additional 20,000 tons of food and, if we optimistically assume that this can be produced at the rate of ½ pound per square foot per year, then we must open up to agriculture, in each year, 3 square miles for each day's increase in the world's population, or for each year's increase, nearly 1100 square miles. Evidently this can also be accomplished in part by an increase of productivity of the land now under agriculture. Of course, I am ignoring here for simplicity any increase in the production of fish although it may well work out, upon examination, that an increase in the production of fish would involve an approximately proportional increase in the use of land for wharves, freezing plants, etc. It would appear then that what we need to set up are balance sheets for various types of foods and for the various regions of the world and, on the basis of the forseeable events, demonstrate the changes which must be made in production, at the same time taking into account the needful improvements in the nutritive status of the earth's population. Since this will involve not only areas which are producers of surplus food, but food deficiency areas, it must in turn be related to the production of industrial items which legitimately enable an area to import its food. Food, however, is only one of the items to be considered. All natural resources must ultimately be taken into account, although not necessarily simultaneously.

It was pointed out a few years ago that Massachusetts east of the Connecticut River has already tapped all of the consequential sources of public water supplies. Such a statement is not one of opinion. It is subject to reasonably exact calculation by engineers and the effect of tapping water supplies outside the area is also similarly subject to accurate estimation. We need balance sheets for water supplies.

This suggests that we need to begin with a team of agricultural experts, plant and animal geographers, geologists, water supply engineers, industrialists, and tying the whole group together, ecologists. The great disadvantage of most attempts to solve problems either on a local or wide scale has been the tendency of politicians to look at the problems from the standpoint of their constituents alone and to seek primarily to alleviate the most painful symptoms without any conception of the effects of that alleviation upon either other symptoms or, more important, the causes. I am strongly of the opinion that the ecologists with the assistance of mathematicians are the only people whose habits of thought will enable them to predict to any reasonable degree the effects of the proposed changes, especially on a world-wide scale, and especially on other and not always closely related problems.

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CYTOLOGY IN 1943

A Review

CYTOLOGY today is at a turning point from which it is moving into a third major phase of development. It began as a descriptive science, and that phase has left indelible marks (and some serious handicaps to modern thinking) in its terminology. In the second phase there was a bifurcation into "experimental cytology" and cytogenetics as well as a continuation of the descriptive phase as a branch of histology. Now cytology must become a part of developmental biology, must become functional with all that that involves in encompassing the data and the concepts of chemistry, physics, genetics and physiology, and the employment of statistical methods of analysis. Yet it must remain descriptive also and never get too far from its historical basis if it is to preserve any measure of unity.

To abstract the "fundamentals" from such a subject and present them in a scant 250 pages is the gigantic task that Professor Sharp has essayed.* His task, difficult enough on account of the territory to be covered, is made incalculably harder because within the field there is sharp divergence of method. Some schools stress detailed and accurate description "without theory." Others argue that properly constructed theories may be more significant than isolated "facts" of direct observation. And, unfortunately, the minds and hands best at direct observation and description are rarely best at theory forming or generalization or abstruse reasoning. The measure of success Professor Sharp has achieved in his ambitious effort depends upon the point of view from which it is considered.

As a condensation of the bulk of the reliable observations made during the first two phases of cytology, the present reviewer considers it remarkably successful; its somewhat disproportionate citation of plant work is his only major criticism. This is most serious in the account of reproduction where 18 pages are devoted to animals of all types and 32 to plants.

But should a book which attempts to establish "fundamentals" be so much of a condensation? Should not more emphasis be placed on modal or "typical" behaviour and specific references be given to exceptions and deviations therefrom? For instance, is it possible to give an account of all the complexities of transmission genetics (cytogenetics) in diploids, polyploids and also aneuploids and other chromosome aberrants within the space of 58 pages? Or of experimental taxonomy and its interrelationships with cytology in 15? This reviewer is of the opinion that to be successful in presenting "fundamentals" in a textbook of this size, the writer must be much more selective; Professor Sharp has, despite his intense condensation, naturally had to leave out much; he should have left out more. To his own classes or to the students of other widely read teachers of cytology who are able both to select and amplify, the present book will be very valuable. Students on their own or teachers who are not specialists in cytology and genetics will wish that Professor Sharp had done more selection for them and at the same time either have amplified many points or given more detailed references to where amplification could be found.

Professor Sharp, in keeping with his objective, makes almost no attempt to outline the newer phases of cytology now developing, such as cyto-chemistry. He does, however, very frequently indicate the directions in which current researches are taking off from the established bases, and emphasizes the importance of selecting the best materials for different ends. In this he achieves one of his obvious purposes of aiding the beginning research student to develop soundly.

**Fundamentals of Cytology*, by Lester W. Sharp. New York and London: McGraw-Hill Book Co. 1943.

Scant attention is paid to theories; one gathers that he feels there has been too much speculation in cytogenetics during recent years. His is as far as possible the inductive, not deductive, approach. Regardless of one's opinion on the degree to which induction or deduction should predominate or interplay in research, the emphasis on data and neglect of theory is justified in an attempt to establish "fundamentals" and is therefore appropriate here. The outline on pp. 115-117 of what we don't know about meiosis is a most useful corrective to the current acceptance as fact by so many geneticists of theories that, whatever their value in teaching or research, are still largely mental concepts of their originators. Unfortunately, far too many very useful working hypotheses have in recent years through constant citation come to be regarded as established fact, or even as data—thereby, of course, reducing their usefulness. It is good to have Professor Sharp make as clear a distinction as is possible between observation and conclusion therefrom in a science in which theory often determines or limits what is seen. The emphasis laid on the difficulties and complexities will not deter the best young workers from tackling the many unsolved problems of meiosis or mitosis, though we must recognize that many advances in science, as in warfare, have been made by men who either didn't know or who refused to recognize the obstacles.

In general, Professor Sharp uses well-accepted terminology. He is conservative in retaining the term "kinetochore" which was suggested in a footnote of his earlier book but has not gained wide acceptance. This reviewer doesn't like the word but considers it better than the widely accepted term "centromere" which is used by most geneticists to indicate the attachment *region*, though its originator defined it as a particle and has since used it in both a spatial and substantial sense and has also coined other terms, "attachment chromomere," and, more recently, "centrogene" for the *particle*. Sharp has adopted the term kinosome, proposed by the reviewer for the particle, but not his "kinomere" for the region which, as a functional whole, is the usual concern of the geneticist. This is not the place for discussion of the relative merits of the various terms used, but it is appropriate to point out that current usage has led to confusion in thinking on problems of chromosome mechanics and to a divergence between descriptive and functional terminology. In the use of x for the gametic chromosome number and n for the "true monoploid number" Professor Sharp reverses the usual procedure; since the former is known and the latter often an unknown, the change does not seem appropriate. Monoploid is also an unnecessary change, as Professor A. H. R. Buller is showing in an interesting note which he is publishing shortly on the etymology of the alternative term "haploid."

In the discussion of chromosome structure, p. 90, a very clear distinction is made between the three levels at which gene, chromonema and chromosome reproduction and separation must be considered. Much fruitless discussion will in future be averted if these are taken to heart by all cytologists and geneticists. If all elementary genetics text-books would as clearly state (p. 227) "when characters are the same in successive generations [they] are said to be inherited, although this really means they have been redeveloped in the offspring because its protoplasm is like that of the parent" there would be less misunderstanding of genetic concepts by medical men and others. In other instances also Professor Sharp does much to clarify and sharpen fundamental concepts.

To summarize: this reviewer considers that Professor Sharp has essayed an extremely difficult, if not impossible, task in the space available to him, but has written a most useful book. It is doubtful if anyone else could have done as much towards realization of the avowed objective. Considering the complexity and amount of material covered there seem to be remarkable few errors.

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STUDIES OF QUADRUPLETS

VII—The Schenses, Four-Egg Quadruplets

IVA C. GARDNER AND H. H. NEWMAN

THE Schense quadruplets, dealt with in this paper, are the sixth set of living quads reported by the joint authors of these studies. They are the second four-egg set dealt with in this series, the first being the Perricone quadruplets.[1]

The authors know of only one other set of four-egg quadruplets who have been the subject of a research report, the Swiss Gehri quads studied by the distinguished anthropologist Professor Otto Schlaginhaufen.[2] All four of the Perricone quadruplets were boys. The Gehri quads, like the present case, have an even distribution of the sexes.

We cannot do justice in a brief summary to Schlaginhaufen's monographic report of the Gehri quads. It covers 90 pages, and includes 7 plates and 11 pedigree charts of various branches of the families of the parents. Much space is devoted to the problem of the inheritance of the twinning tendency. From the data derived from the pedigrees, the author concludes that the twinning potentiality is inherited as a simple recessive trait. The pedigree of the mother of the quadruplets shows twelve instances of twinning in collateral lines. The mother of the father of the quads is regarded by Schlaginhaufen as surely homozygous for the twinning trait. How the father could have any influence on the multiple ovulation of his wife is not explained.

The Gehri quads, Oscar, Bertha, Rosa and Arthur, were 60 years old when Schlaginhaufen studied them. They were diagnosed as four-egg quadruplets on the basis of differences in their dermatoglyphics, in their physical characteristics and in temperaments. Though resembling each other somewhat more than they do their other brothers and sisters, they are still very different physically, temperamentally and in the occupations they have chosen. Apart from the fact that it is remarkable to find a set of quadruplets all alive at an age of sixty, the Gehri quadruplets did not greatly illuminate the problem of heredity-environment. Our brief and cursory note regarding the Schenses may seem trivial when compared with Schlaginhaufen's monumental study of the Gehris. It may, however, serve as a datum point for comparison when, in the years ahead, the Schenses achieve a Schalginhaufen.

Birth and Parentage of the Schense Quadruplets

Joan, Jean, James and Jay were born in St. Luke's Hospital, in Aberdeen, South Dakota, January 13, 1931. Dr. W. D. Farrel, county physician, officiated. The father of the quadruplets was a farmer of German extraction, who had a rented farm near Aberdeen. Like so many tenant farmers Mr. Schense found it difficult to earn a livelihood, and the arrival of four more children added a severe burden. For the first eight years little help was forthcoming from the community, but in 1939 certain public-spirited people of Aberdeen decided to do something handsome for the quadruplets. They elected a "Schense Quadruplet Control Committee," whose object was to promote the general welfare and cultural development of the four children. A tag day during Education Week in 1939 brought in over $2,000 to finance the project. Had this help come sooner it would have been of greater benefit and would have made a great difference in the circumstances of the family.

At any rate the quadruplets were moved to Aberdeen, where they lived in comfortable quarters and were given everything necessary for their health and happiness, including exceptional educational opportunities. It was not long, however, before the Schense parents became dissatisfied with the arrangement.

THE SCHENSE QUADRUPLETS

Figure 5

Joan, Jean, James, and Jay at nine years seven months of age. These children differ from each other in a large number of characteristics, and there is no doubt that each of them arose from a separate fertilized egg. Eye colors vary from light blue, through hazel, to brown. Hair colors range from light brown to medium brown. In intelligence these quads seem to be rather more similar than they are in physical appearance.

They feared, quite naturally, that a long separation from the rest of the family might bring about a breach between the quadruplets and their brothers and sisters on the farm, who were not invited to share the fine opportunities the quadruplets were enjoying. The result was that after spending a little more than a year as the guests of the Committee, the quadruplets returned to their home and have remained there ever since.

From the somewhat sketchy account at hand it appears that the Schenses had three children before the quadruplets more than doubled the size of their brood. Times were hard on the farm, and some years after the birth of the quads Mr. Schense endeavored to improve his situation by moving to a farm near Hecla. There the family still lives. When the quadruplets were eighteen months old their mother died. About a year later their father remarried. The second Mrs. Schense had been the nurse-housekeeper during the quad's infancy. She remains very fond of them, even though she has since had three children of her own. The family now consists of three children older than the quadruplets, three younger, and the quadruplets themselves. Life on the farm has been a struggle and all have had to live like Spartans to make ends meet.

Zygotic Diagnosis

At the time of their birth, newspaper writers mistakenly stated that the Schense quadruplets consisted of "two

"SIBLINGS" WITH THE SAME BIRTHDAY
Figure 6

Showing rather more genetic diversity than is encountered in many groups of brothers and sisters, these four children have grown up in a relatively standardized environment in the sense that the usual age differences characteristic of siblings do not exist.

pairs of identical twins, a pair of boy twins and a pair of girl twins." Such a diagnosis might have been excusable when the babies were new-born, but at the present time, as anyone can see from the photograph (Figure 5) they are very different from one another, without even a strong family resemblance. Some claim to see a closer resemblance between Jay and Jean and between James and Joan.

TABLE I. Physical Characters of the Schense Quadruplets

Characteristic	*Joan*	*Jean*	*James*	*Jay*
Standing height	132 cm.	134 cm.	137 cm.	140 cm.
Sitting height	69 "	71 "	72 "	73 "
Head length	16.7 cm.	17.5 cm.	16.5 cm.	17.7 cm.
Head width	13.0 "	14.0 "	13.2 "	14.5 "
Cephalic index	78.8	80.0	80.0	81.9
Eye color	hazel	light blue	hazel	light brown
Hair color	light brown	light blond "candy color"	medium brown	light brown
Skin color	slightly dark	very fair	sun tan	slightly dark
Dentition	very irreg. 13 out	reg., smaller than any of the others	larger than any of the others, irreg.	reg., but widely spaced
Handedness	right	right	right	left
Hair whorl	clockwise	same	same	same

but the various sets of photographs at our disposal do not, in our estimation, show such resemblances. It is our conviction that diagnosis of this group as a four-egg set could be made conclusively on the basis of the photographs alone, but it seems advisable to present the remainder of the data usually employed in diagnosing multiple births. The following table (Table I) gives some of the physical characteristics of the Schense quadruplets as they were on August 15, 1940.

In addition to the data in Table I, it should be said that James and Jean are more robust than the other two. Joan has had some heart trouble, has had measles and chicken pox, which the others have missed. She has had more colds than the others. Jay, the left-handed member, has a noticeable speech defect.

Dermatoglyphics

Although the available palm and finger prints are somewhat imperfect, they permit of the formulations shown below.

Since there is no possibility that either of the boys is a one-egg-twin partner of either girl, the only point at issue is whether the two boys or the two girls might be one-egg twins. This possibility with respect to the two girls is quickly dismissed when one examines the prints, for these are about as different as they well could be. On the basis of formulae alone, however, the two boys could be classed as monozygotic. Their right palm prints have almost exactly the same formulae and the two right palms are more alike than either right is like his own left. The finger print formulae of the two boys correspond in eight out of ten items, and therefore might fall within the range of the Stocks' test of monozygosity. This is a good example of the many cases we have handled in which similarity in formulae can be misleading as aids in the diagnosis of zygosity, especially when the formulae happen to be among those most commonly found. When actually placed side by side, the two right palms are not similar at all. The finger prints also are much more different than the formulae indicate, for the ulnar loops on all of James' fingers are fairly large patterns with a relatively high ridge count, while those of Jay are small, flat and with low ridge count. Unfortunately these finger prints were not rolled separately and sometimes do not include the complete pattern, rendering accurate ridge counting impossible. It is certain, however, that the discrepancy in numbers of ridges seen in the fingers of the two boys far exceeds that in any pair of one-egg twins we have encountered.

In view of the data presented above we would feel justified in diagnosing the Schenses as four-egg quadruplets on the basis of the photographs alone, on the basis of a combination of four genetic features (eye color, hair color, skin color and dental peculiarities), or on the basis of dermatoglyphics alone. With all three types of criteria in agreement, this diagnosis may be considered unequivocal.

Results of Mental Tests

Three standard mental tests were given the Schense quadruplets when they were nine years, seven months old. The results of these tests are summarized in Table II.

Palm Prints

	Left	*Right*
Joan:	9-9. 9. 5".5'-t-A^u/A^c.O/L.O.L.D	11. 9. 5".5'-t'-A^u/A^c.O.O.L.V.
Jean:	7(8).5"(6).5".4-tt'-A^u/L^u.O.O.O.L	7(8).5"(6).5".4-t'-A.O.O.O.L
James:	7. 9. 5'.2-tt'-A^u/L^u.O.O.L.L	9. 7. 5".4-t'-A^u/A^c.O.O.O.L
Jay:	9. 9. 5".2-tt'-A^u/L^u.O.O.l.v.	9. 7. 5'.4-t'-A^u/A^c.O.O.O.L

Finger Prints

	Left	*Right*
Joan:	U. A. U. U. U	U. U. U. W^{lu}. U
Jean:	U. R. U. W^{lu}. W	U. A. A. U. U
James:	U. U. U. U. U	U. U. U. U. U
Jay:	U. A. U. U. U	U. U. A. U. U

On the Stanford-Binet test Jay ranks first, one point ahead of Joan. James was nine points lower than Jay and Jean was nine points lower than Joan. These differences between the same-sexed pairs are about the same as the average difference between fifty pairs of two-egg twins reared together or that of twenty pairs of one-egg twins reared apart.

On the Army Beta test Joan ranks distinctly highest, James and Jay next with equal scores, and Jean is considerably the lowest, as she was on the first test.

On the Stanford Achievement test the ranking is as follows: James, Jay, Joan and Jean. There is little to choose among the first three, but Jean again is distinctly the lowest. On the basis of all three tests, it appears that Joan, James and Jay are approximately equal in mental ability, while Jean scores consistently lower, though still above the average for her age group. Dr. Gardner is inclined to attribute Jean's relatively low standing to the fact that she has a more sociable and fun-loving disposition and makes less of an effort to excel in school work. It might be noted that, although the Schenses were a year younger than were the Morlok quadruplets when they took the same tests, all of them outscored any of the Morloks. The Schenses, however, took the tests after they had had the benefit of unusual educational opportunities afforded by the Control Committee mentioned above. This might be regarded as a boost for the special educational methods employed, but in the absence of tests before this period we cannot be sure that such a claim would be justified.

TABLE II. Mental Test Scores of the Schense Quadruplets

		Joan	*Jean*	*James*	*Jay*
Stanford-Binet					
(Form L)	M.A.	11	10/2	10/4	11/2
	I.Q.	115	106	107	116
Army Beta	M.A.	12/10	11	12	12
	I.Q.	134	115	126	126
Stanford Achievement					
Reading					
Paragraph mean.		33	30	36	36
Word meaning		56	43	56	44
Dictation		27	20	27	30
Arithmetic					
Reasoning		53	48	67	67
Computation		47	47	53	56
Total Score					
Aver. of five		43.1	37.6	47.8	46.4

Dr. Gardner's notes contain no special comments about the personality traits of the four children except that Jean is distinctly the liveliest and the most sociable of the four; and that Jay's speech defect tends to make him somewhat diffident. The truth of the matter seems to be that there was not much point in trying to compare with one another four youngsters as different in personalities as they are in their physical traits.

Were the Schenses Originally Quintuplets?

Jay is a left-hander with a type of speech defect characteristic of left-handers whose asymmetry is partially reversed. He is also reversed as to his palm-pattern asymmetry, for his left palm is more dextral in its patterns than his right. In brief, he has some of the characteristics of a partially reversed member of a one-egg twin pair. It may well be that his original one-egg twin partner died early in the course of development, leaving Jay as the only representative of the twinning zygote from which he was derived. If Jay originally had a one-egg twin partner, as seems not unlikely, the Schense quadruplets were originally quintuplets.

Summary

The Schense quadruplets are the third four-egg set to be studied and reported within recent years. It appears that we were wrong in our original opinion that the ovulation of four eggs at once, their successful fertilization, implantation and placentation, gestation, birth and survival as healthy individuals, was a highly improbable event. As a matter of fact, four-egg quadruplets seem to be commoner than any other zygotic type. Prenatal crowding and competition have apparently done no harm to the members of the three sets of four-egg quadruplets that have been studied. There is no suggestion of anything like the freemartin

effect such as is common in cattle twins of opposite sexes, although in this set of two males and two females there must have been ample opportunity for anastomoses of placental blood vessels.

In general, the Schense quadruplets seem to be in no way different from four siblings except that they are of the same age. Being reared together under essentially identical environmental conditions has apparently not caused them to grow more similar. They are today a strikingly dissimilar group, hardly enough alike to suggest to one viewing them without knowledge of their relationship that they are even brothers and sisters.

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BIG TREES — 1915 AND 1943

LATE in 1914 the American Genetic Association offered prizes for photographs and authenticated information about large trees. Several dozen sizeable giants were measured and photographed and the ten at the top of the list got their pictures and records of dimensions recorded in the JOURNAL for September, 1915.

The American Forestry Association has recently issued a more ambitious list of giants comprising the largest recorded representatives of 221 species of forest trees growing in the United States. The greatest circumference is that of the General Sherman Sequoia (101 feet, 6 inches); the tallest is a redwood growing in Humbolt County, California, measuring 308 feet. Some of the giants are of much more modest proportions. At the other end of the size array are an Eastern Wahoo with a circumference of one foot, and a Pagoda Dogwood with a circumference of eight inches.

The American Genetic Association contest was limited to hardwoods. The largest tree reported in 1915 was a sycamore in Indiana, 42 feet, 3 inches in circumference 5 feet from the ground. The new title-holder is a sycamore (Planetree) in Ohio, 42 feet, 7 inches in circumference. If the Indiana specimen is still living, it would very likely have exceeded that record by this time. Seven species are listed in both the 1915 record and the 1943 record; the comparison between them are as follows:

Species	*1915*	*1943*
Catalpa	16′ Ark.	17′-10″ Md.
Chestnut	33′-4″ N.Car.	27′-3″ Tenn. (dead tree)
Elm	28′ Conn.	30′-3″ Conn. (same tree)
California Valley Oak (Quercus lobata)	37′-6″ Cal.	28′-3″ Cal.
Pecan	19′-6″ La.	21′-4″ La.
Sassafras	15′-10″ Pa.	17′-2″ Ohio
Tulip Tree	34′-6″ N.Car.	26′ Md.

The Wethersfield Elm is the only tree which is included in both lists. It is supposed to have been planted in 1734. With the General Sherman Sequoia, it probably shares the honor of being America's most prominent tree. A dead elm stump was reported in 1915 33 feet in circumference.

The size of the forest giants does not seem to have changed greatly in the last 30 years. One species outstanding for size, the chestnut, has virtually disappeared from America and some introduced species are reaching goodly stature, notably the eucalyptus trees of California. But this list contains only native trees and includes no plant immigrants.

The American Forestry Association is interested in learning of other trees which approach or exceed the dimensions of those given on this list. Copies of it can be obtained from the office of that Association, 919 Seventeenth Street, N. W., Washington 6, D. C.

THE INHERITANCE OF SOME QUANTITATIVE CHARACTERISTICS IN TURKEYS

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EASILY noticeable variations in quantity and shape of breast fleshing, body weight, and shank length are familiar to most persons who have occasion to handle turkeys. These variations partly determine carcass quality and percentage of edible flesh. That they may be genetically determined is indicated by the fact that breeders have succeeded in modifying them through mass selection of breeding stock. The amount of breast flesh has been increased by this procedure, and desired changes have been achieved in body weight and shank length. Mass selection could effect little or no change in such characteristics unless there existed a definite (though not necessarily high) correlation between the phenotype and the genotype governing a particular characteristic. In order to establish the inheritance of the three quantitative characteristics mentioned with some degree of exactness, the present data were compiled for the years 1940, 1941, and 1942.

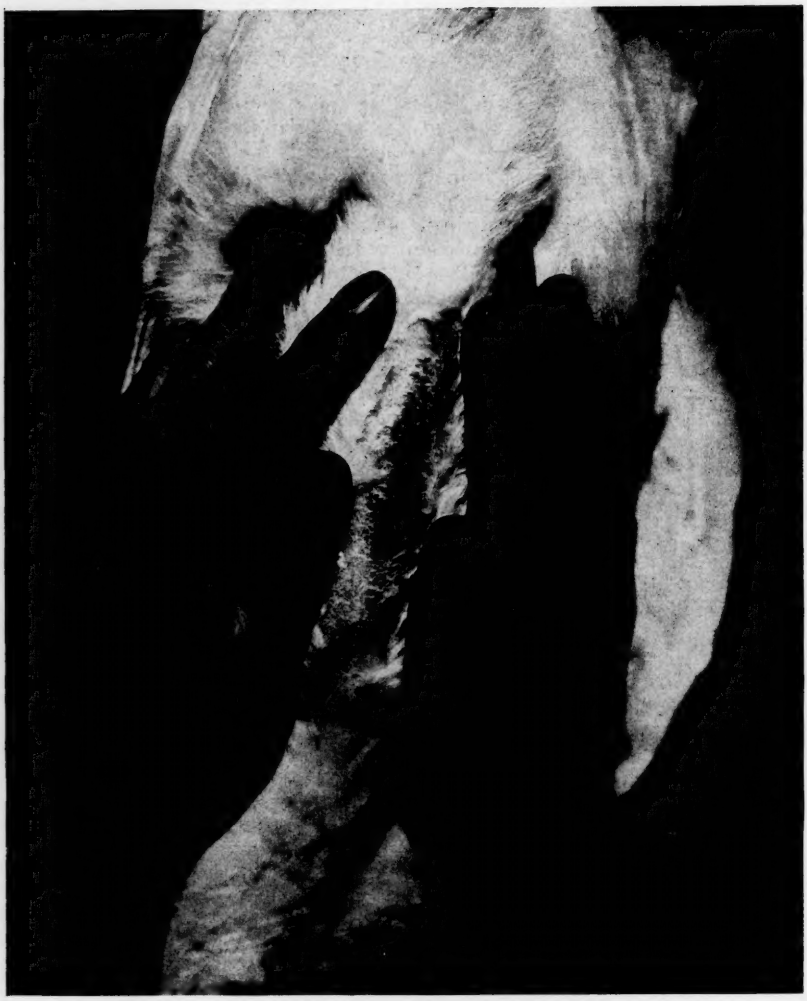
Four varieties of turkeys were used: 190 Standard Bronze, 179 White Holland, 161 Broad Breasted Bronze, and 1125 Beltsville Small Whites. Included in the study were 58 F_1's and 41 F_2's of a Broad Breasted Bronze $\times$ Beltsville Small White cross, making a total of 1754 turkeys. The stock used for the first three varieties was purchased from well-known breeders; the Small Whites originated at the Beltsville Research Center.

Breast Type

One of the first objectives of the experiment was to find a method of measuring breast variations that could be used in comparing turkeys hatched at different times and in different years. Observations of breast development were made on all turkeys of both sexes at 24 weeks of age. The breast fleshing was observed as depicted in Figure 7, the length of the breast, the breadth, amount of fleshing, and shape of the breast being estimated. In grading turkeys for breast type, an assistant holds the turkey on its back in his lap, the head of the turkey toward the grader who parts the breast feathers, then runs his hands over the musculature. By a combination of the impressions gained through touch and sight, breast grades are assigned the specimen. The grades shown in Figure 8 represent the three major breast grades, broad, medium, and narrow, that were used. These are subdivided by using plus and minus grades for each of the major grades, thus making a total of nine grades, broad plus, broad, broad minus, medium plus, medium, etc. These grades were given numerical values from 1 to 9, 1 being the most desirable type and 9 the poorest. This method, if carefully followed, is suitable for grading turkeys for breast development.

In the average turkey, breast musculature is broadest at the forward tip of the keel and narrows gradually toward the rear point of the keel. The turkeys are first assigned a breast-grade in relation to the shape of the musculature near the front of the keel. However, the breast musculature of some turkeys narrows very rapidly and produces a pronounced inverted V-shaped breast. Such a conformation was considered to reduce the grade one or two points from that allowed for the breast shape at the front end of the keel, depending on how rapidly the breast shape narrows. This tendency to narrow is marked in birds with

*Now on military leave and serving with the United States Army.



METHOD OF MAKING OBSERVATIONS

Figure 7

In grading the breast development of turkeys, an assistant holds the turkey on its back in his lap. The grader then evaluates development by appearance and "feel." Breast grade can be assigned with a considerable degree of accuracy as demonstrated by concordance of independent evaluations by several graders.

medium to heavy breast musculature; the narrow-breasted birds are not affected. Turkeys within such types graded "broad plus" (1), "broad" (2), "broad minus" (3), and "medium plus" (4), are considered desirable, those with "medium" and "medium minus," acceptable, and the remainder are classed as undesirable breast types. The breast grade of turkeys at 24 weeks of age was accepted as the final grade, as subsequent checks showed little change in status later in life. It was also noted that the method of grading for breast type in each sex produced similar grades for similar types; therefore, the data for both sexes could be placed together.

Figure 9 shows two views of typical dressed Broad Breasted Bronze and Beltsville Small White turkey toms used in this study. The parental cross, Beltsville Small White toms with Broad Breasted Bronze hens, was used in obtaining the F_1 generation.

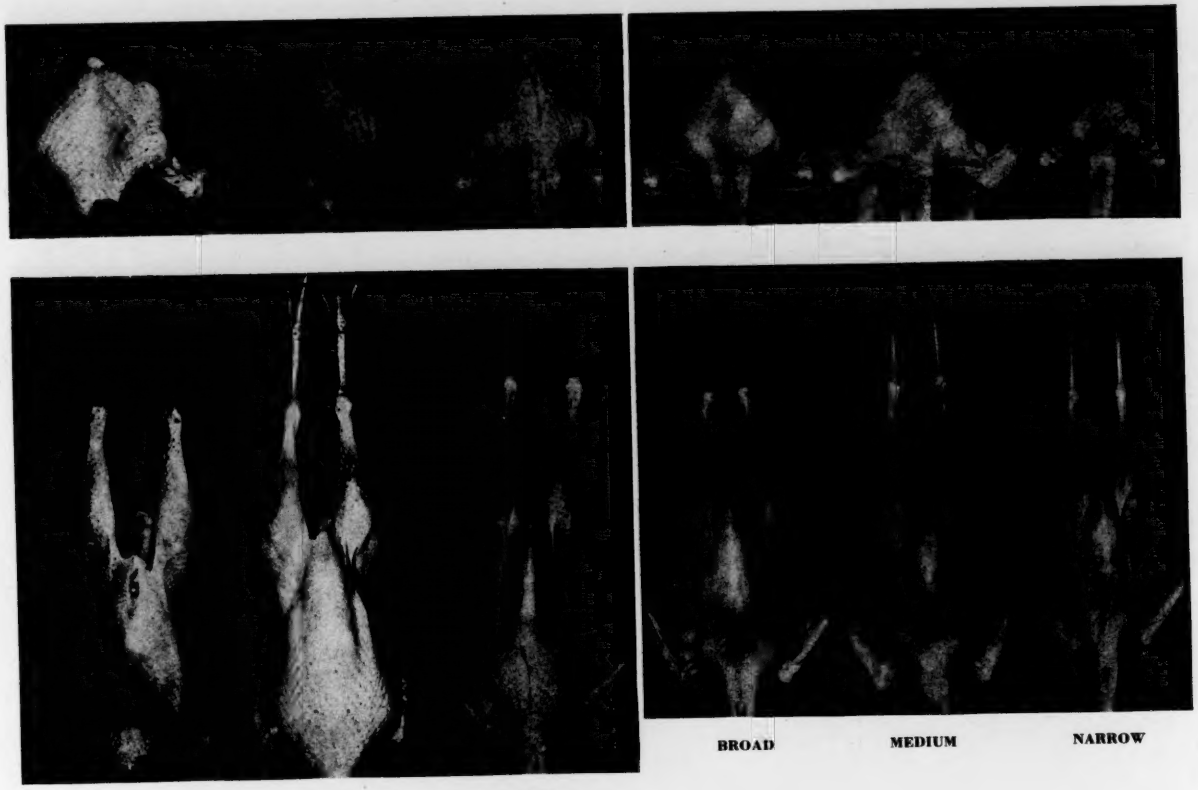
Figure 10 shows the distribution of individuals according to breast grade for the four varieties and the hybrid studied. These data are for the particular strains used and the results might differ for other strains of the same varieties of turkeys. Asmundson and Lerner[2] showed that in three strains of Bronze turkeys there were differences between the strains of 893 grams in live body weight at 24 weeks of age and 0.27 cm. in shank length. The Standard Bronze turkeys used in this study had an average breast type of 6.16, (medium minus = 6.0), the White Hollands 5.87, the Broad Breasted Bronze 3.61 (medium plus = 4.0), Beltsville Small Whites 4.8 (medium = 5.0). The F_1 and F_2 progeny of the Beltsville Small White crossed with Broad Breasted Bronze had an average breast type intermediate between that for the parental strains used, being approximately 4.1. These observations on live birds confirm the data of Harshaw, et al[3] on the ratio of breast muscle to dressed weights found in the same four varieties, namely "the breast muscle averaged a little more than 22 per cent of the dressed weight in the Broad Breasted Bronze, a little more than 19 per cent in the Beltsville Small White, and slightly more than 18 per cent in the Standard Bronze and White Holland. Thus, in the same weight of dressed turkeys, the Broad Breasted Bronze would supply 20 per cent and the Beltsville Small White five per cent more breast meat than the Standard Bronze and White Holland."

The data for F_1 and F_2 progeny of the cross Beltsville Small White turkeys $\times$ Broad Breasted Bronze indicate that breast fleshing may be influenced by breeding. The F_1 progeny represents a marked improvement over that of the normally fleshed turkey. The F_2 generation was very similar to the F_1 and was only slightly more variable.

From these data it is evident that the development of breast fleshing is inherited and that turkey varieties can in general be improved in this respect by proper methods of selection and breeding. Although the mode of inheritance seems to be complicated it appears that the association between phenotypes and genotypes is close enough so that improvement in breast fleshing may be accomplished in relatively few years of breeding.

Body Weight

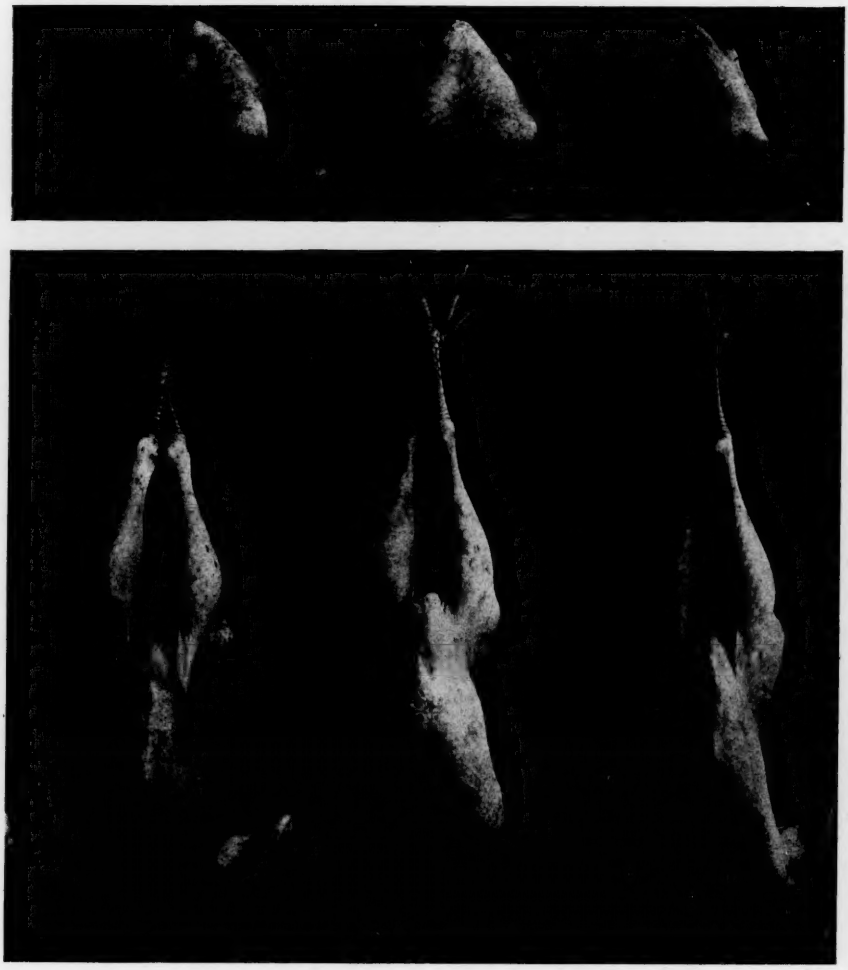
The distribution of weight of all birds of both sexes at 24 weeks of age is given in Figure 10. Like breast conformation, body weight behaves genetically as a quantitative characteristic conditioned by several undetermined genes. The F_1 and F_2 progeny are intermediate in weight between the two parental strains. Although the F_1 body weights indicate a blending inheritance, the F_1 and F_2 more closely approach the body weights of the Beltsville Small Whites than those of the Broad Breasted Bronze. Asmundson[1] obtained similar results in crossing White Holland turkeys with Black, where there was a difference of approximately 500 grams in the body weight of the males, and 200 grams in the females at 24 weeks of age. Asmundson reported another cross of Black with Bourbon Red turkeys wherein the average weight of the progeny was greater at 24 weeks than that of either parent strain which is contrary to the present



THE THREE MAIN BREAST GRADES

Figure 8

The grades for males (left) and female (right), "broad," "medium," and "narrow," are shown here. In practice these are divided so that there are nine sub-grades. By breeding from the broad and "medium plus" grades, a rapid change in the degree of breast musculature was achieved.

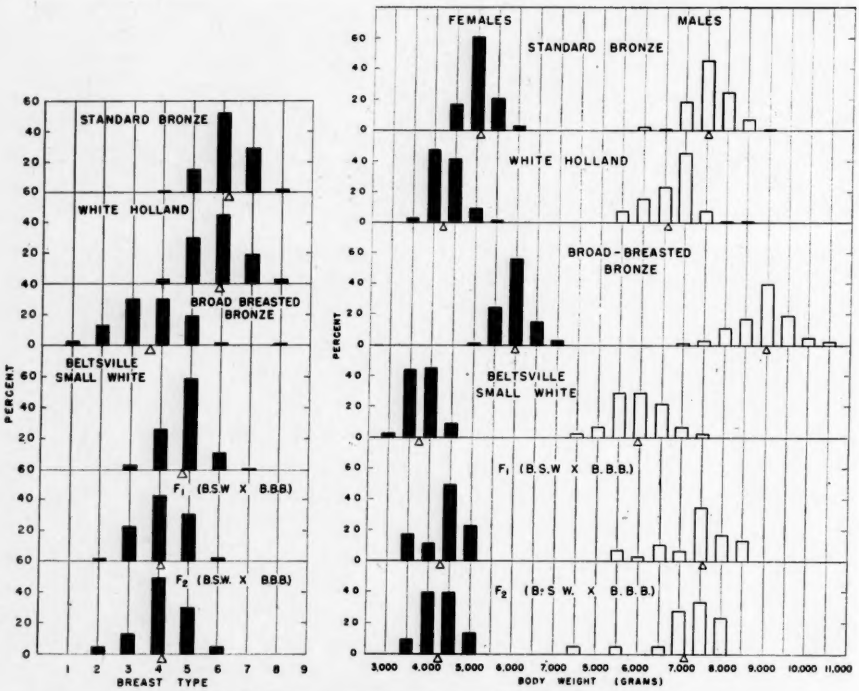


RESULT OF SELECTION FOR BREAST DEVELOPMENT

Figure 9

Selected examples of broad-breasted bronze tom turkeys are shown at the right and left, with a Beltsville Small White tom in the center. The objective in the development of the Beltsville Small White was a bird having a lesser body weight than the average and a greater breast development. This dual objective was achieved in about five years of selective breeding.

data. The disparity between the latter finding and the others reported above may be due to the fact that the Black and Bourdon Red were similar in weight The enhanced weight of the hybrids was possibly due to heterosis. The differences in body weight of the turkeys used in this study were greater than in the crosses reported by Asmundson. This should be considered as a major factor in accounting for the differences noted between the results of the two experiments. In the present studies, the differences between the live weight of the



DISTRIBUTION OF BREAST TYPE AND BODY WEIGHT

Figure 10

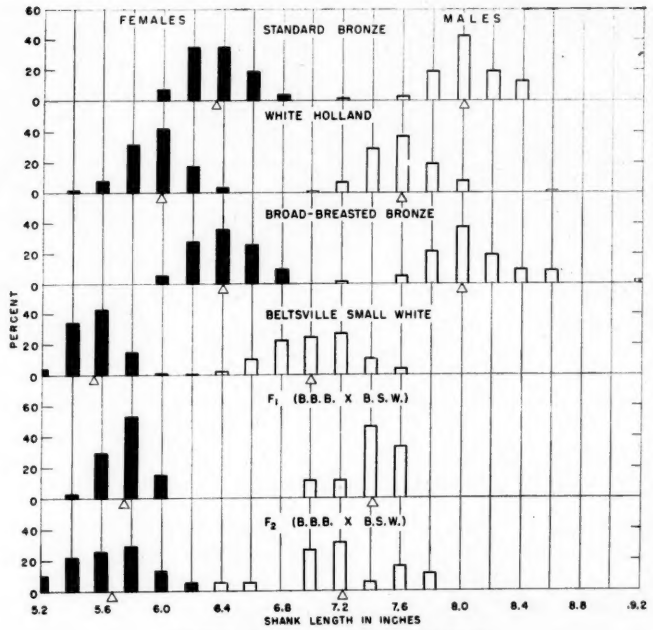
The distribution of three varieties of turkeys and of two generations of crosses between two of them are given. Breast type is proved on analysis to be independent of sex so that the sexes are combined with respect to this characteristic. Weight for females and males is presented separately. The triangles below the base-lines show the means for each series.

males of the parental breeds at 24 weeks of age was 2,983 grams, and of the females, 2,179 grams.

The inheritance of body weight, therefore, seems to be similar to the inheritance of breast type, and again the association between phenotype and genotype is close enough to enable the poultryman, by proper selection and breeding methods, to obtain turkeys of any body weight within wide limits and in a reasonably short time.

Shank Length

Breast type and body weight have been given more attention in breeding programs than shank length. Hence, greater variation in shank length of turkeys may be expected. As shown in Figure 11, shank length was more variable in both sexes than either of the other two characteristics. Shank length may be quite important, especially insofar as it is related to body type and length of neck. In Figure 12 the bird with the longest shanks had the longest neck; the one with the shortest shanks, the shortest neck, and that the shanks of the others were in proportion to the length of the necks. Figure 9 also illustrates the association of shank length and body weight. The Broad Breasted Bronze have longer shanks than the Beltsville Small Whites. Japp, Thompson, and Milby[5] also noted this association and stated that progeny selected as superior on other criteria have proportionately shorter shanks and less body depth at all ages.



SHANK LENGTH INHERITANCE

Figure 11

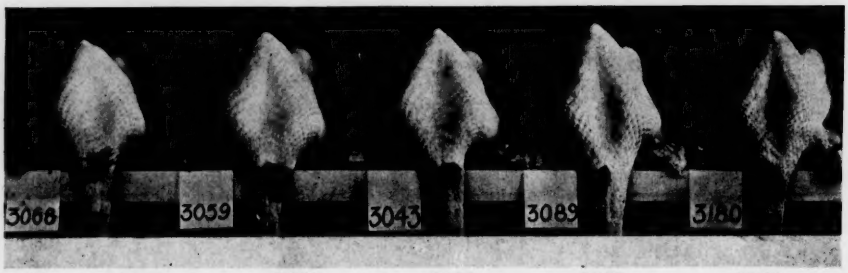
Shank length shows rather more "spread" than the other characteristics studied. This is greater among the males than among the females. The preponderance of short shanked females and the bimodal distribution of males in the F_2 generation of the cross indicates that some of the factors for short shank tend to be dominant in inheritance.

Figure 11 indicates that shank length also shows the "blending inheritance" of a quantitative characteristic, with some dominance of the short shank factors. It is evident that shank length is a heritable characteristic for which turkeys are highly heterozygous, so that the phenotype is quite variable. Since it appears that short shanks tend to be dominant, and their inheritance relatively simpler than the other qualities studied, it is possible to affect length of shanks through selective breeding in a relatively short period of time.

Discussion

All three characteristics studied show blending inheritance in the F_1 and F_2 generations and lack of definite segregation into clearly defined classes in the F_2 generation. In the case of live body weights at 24 weeks of age and of shank length, there is some evidence of dominance of the factors for light body weight and for short shanks. There is sufficient relationship between the phenotype of the individual and the underlying genotype to make possible a confident prediction that selective breeding based on mass selection will achieve definite goals in a relatively short period. Within five years one can have a breed of turkeys "gene-tailored" to any desired weight, breast-form or shank length within the observed range of variation of these characteristics.

As these quantitative characteristics are undoubtedly controlled in their expression by many genes, it might be feared that because definite individual genetic factors have not been isolated it would be practically impossible to im-



Number	3068	3059	3043	3089	3180
Body Weight	5100	5800	6260	6010	5610 (grams)
Shank Length	6.6	6.3	7.3	7.1	6.6 (inches)

RESULTS OF SELECTION PROJECT

Figure 12

Directly under the individuals shown are given the body weights and the shank lengths. Breast conformation is satisfactory ("medium plus" or better) in all individuals shown. The animal breeder can expect rapid progress in selecting for characters conditioned by several genes if the relation between phenotype and genotype is fairly definite. When dominance and recessiveness interfere with this direct relation, mass selection may not be so successful.

prove any of them by simple breeding methods. However, Hazel and Lush,[4] in a recent study, showed that selection for a total score of desirability in respect to a few characteristics is much more efficient than selection for one trait at a time. As a matter of fact, this method has been generally successful in the case of such independent production characteristics as egg production and egg weight in chickens.

Lest the reader be inclined to doubt the possibility that quantitative characteristics such as those discussed above can be modified by selection, a few examples of results achieved may not be amiss. Olsen and Knox[7] and Knox and Godfrey[6] were able to achieve definitely prescribed objectives in improving two characteristics, egg weight and per cent of thick albumen, in four and five years respectively of intensive breeding and selection. The establishment of a strain of small white turkeys with desirable breast conformation was completed within five years. This new breed, the Beltsville Small White, was produced to meet a definite market need, the specifications having been clearly defined before the project was undertaken. From the breeder's point of view, selection will work to produce desired modifications in breed characteristics in all instances wherein there is a definite (though not necessarily complete) correlation between genotype and phenotype. The exact delimitation of the genetic mechanism is not necessary for breed improvement to be achieved.

Summary

Observations were made for breast type, live body weight at 24 weeks of age, and shank length in four different varieties of turkeys. The Beltsville Small Whites were crossed with Broad Breasted Bronze turkeys. All three characters exhibit a "blending" type of inheritance in F_1 and F_2 typical of quantitative characters. The factors for light body weight and short shanks showed some dominance.

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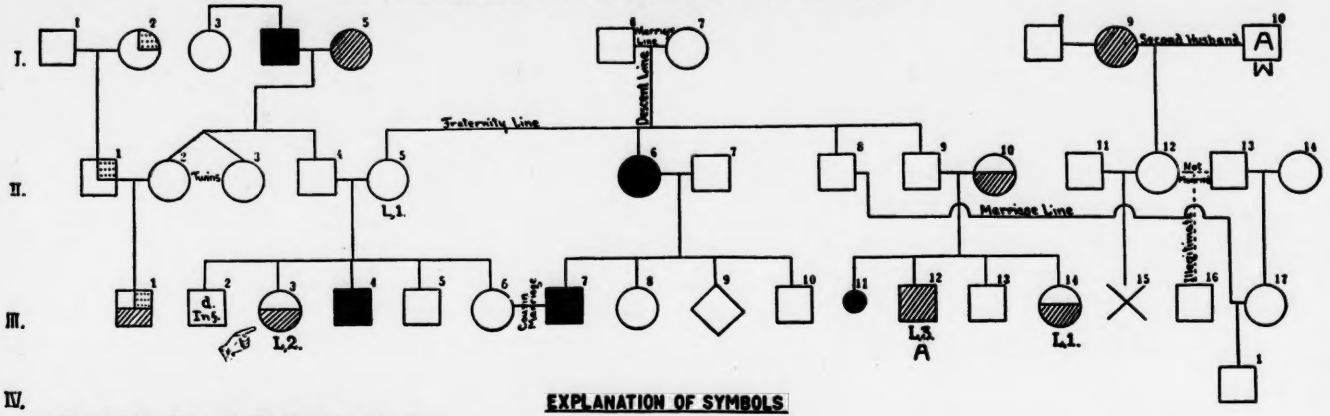

EXPLANATION OF SYMBOLS

(a) **Standard for all Pedigree Charts:**

□=Male; ○=Female; ◇=Sex unknown; ●=Still-birth or Miscarriage; X=Children — number and sex unknown; ○○=Twins; d.Inf.=Died in Infancy; ☞ Points to the Propositus or central figure in the pedigree.

□—○=Parents.

□○□○○=Children.

Roman figures to the left indicate generations; Arabic figures locate individuals, (thus III.7 is the young man in the third generation who married his cousin).

The following letters, placed in or around the individual's pedigree symbol, are standard for certain traits: A, alcoholic; B, blind; D, deaf; E, epileptic; F, feebleminded; I, insane; M, migraineous; N, normal in reference to traits under consideration; Ne, neurotic; P, paralytic; Sx, sexually immoral; S, syphilitic; T, tuberculous; W, wanderer.

(b) **Especially devised or selected for this particular pedigree-chart:**

■● = Successful leaders in politics. ⓤ ⓛ = Extra thumb on right hand. L.1.=Highly successful author. L.3.=Little or no ability in literary efforts. ▨ ◍ = Superior in vocal music. ▨ ◍ = Medium attainment in vocal music.

To fit the particular family and traits (whether physical, mental or temperamental; good or bad) under consideration, invent special symbols, or select special letters (in addition to those standardized under (a) above) to be placed within or near the particular individual's pedigree symbol, to indicate particular traits and their degree of development.

Prepared by the International Commission of Eugenics. See *Journal of Heredity* for August 1926. Additional copies may be obtained from A.G.A.